COMPARATIVE BEHAVIOR OF THE YELLOW-HEADED BLACKBIRD, RED-WINGED BLACKBIRD, AND OTHER ICTERIDS

Robert W. Nero

The Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) is a sexdimorphic, polygynous, colonial, marsh-nesting species whose usual nesting substrate is emergent vegetation, e.g., bulrush (*Scirpus*), cattail (*Typha*), or phragmites (*Phragmites*) in fairly deep water. The species has been studied from several aspects by Ammann (1938), Fautin (1940, 1941*a*, *b*), Linsdale (1938), Roberts (1909, 1921, 1936), Wetmore (1920), and others, and Bent (1958) has a good summary of their reports. Since in none of these studies has the behavioral aspect been of primary concern, however, some basic behavior patterns may still be described for this species.

The following notes are concerned chiefly with agonistic, courtship, and mating displays, and related behavior of the "Yellowhead." Observations were made mainly near Regina, Saskatchewan, from 9 May to 6 June 1957, and from 8 May to 6 June 1958, at irregular periods, but usually in the early morning and late afternoon. In 1957, most observations were made at a small roadside colony (6–10 males) about 7 miles south of Regina, and a few observations were made at a larger but less accessible colony near the southwest city limits. Both of these colonies were destroyed in 1958 as a result of drainage and drought, and in that year I studied a small colony in a cattail marsh near the end of effluent pipes from the City Power Plant (in the Regina Waterfowl Park). The birds in this colony were relatively tame because they were accustomed to workers from the power plant regularly walking along the pipes. I took still and motion pictures throughout the study and made observations from a platform on top of the pipes 10 feet above the water, directly adjacent to three territories. In 1959, this colony was broken up early in the season because of low water levels. I used mounted birds to elicit behavior, and some unexpected and significant behavior resulted.

"Display" is used here in the sense defined by Moynihan (1955*a*:240): "those peculiarly standardized and often exaggerated performances, including all vocalizations and many movements and postures, which have become specialized and modified as social signals or releasers."

The Red-winged Blackbird (*Agelaius phoeniceus*) or "Redwing" has been used to a large extent as a model for comparison, and references are made on this basis throughout this report. For certain displays I have attempted a survey of the icterine literature, based largely on the abundant material recently made available in Bent (1958). I have made comparisons with only

a few non-icterine species and, as a matter of convenience, have relied on a study of the Chaffinch (*Fringilla coelebs*) by Marler (1956).

Certain nomenclatural difficulties were settled by reference to the American Ornithologists' Union Check-list (1957), Eisenmann (1955), Hellmayr (1937), and Parkes (1954).

VOCALIZATION

Male song.—Ammann (1938) and others have described two types of song for the Yellowhead: One is the short "accent song" which has clearly defined syllables and usually involves little plumage erection or body movement. The other is the "buzz song" which begins with short *cow* notes and terminates with a long, sustained "buzz" accompanied by considerable body movement (see Song-spread below). As in the song of the Red-winged Blackbird, the last phrase is given with varying emphasis (Nero, 1956:9–10). It is my impression that the "accent song" is a low-intensity or incomplete version of the "buzz song" given when the motivation is weak. The "accent song" appears often to evoke similar calls from other males. Immature males (first year) occasionally give both songs in much the same way as the adults, though in somewhat more musical tones.

Female song.—Female song (in Song-spread, see below) consists of a series of harsh, nasal, reedy, or buzzy sounds similar to the "buzz" portion of male song.

Call notes, alarm notes, and scolding notes.—(1) *Tsheck*: A short, harsh call note given by both sexes, but harsher and louder in the male, is the most frequent vocalization apart from song. Although its function is not clear it appears to indicate general wariness or alertness and may also help to maintain social bonds.

(2) *Clerrk*: The male has, in addition, this alarm call which is soft, somewhat trilled, metallic, and lower and softer than the *tsheck* call. Males gave this when I approached them, and when confronting a male dummy (but not attacking it). Females occasionally uttered a similar call.

(3) "Hawk call": A shrill, chattering call was often given by the male (with extended neck, ruffled plumage, and spread tail) at the appearance and approach of birds of prey (Fig. 1). This has been noted previously by Wetmore (1920:404), Linsdale (1938:133), and Dawson (*in* Bent, 1958: 116). The reaction to raptorial birds (and others apparently providing a similar stimulus) varied from the soft *clerrk* to a high-pitched, rapidly repeated, and trilled note: *prill-prill-prill*. Such calls were usually picked up and repeated by most of the males in sight. These calls were given by one or more birds to Common Crows (*Corvus brachyrhynchos*) (two occasions), Franklin's Gulls (*Larus pipixcan*) (two), Red-tailed Hawks (*Buteo jamaicen-*

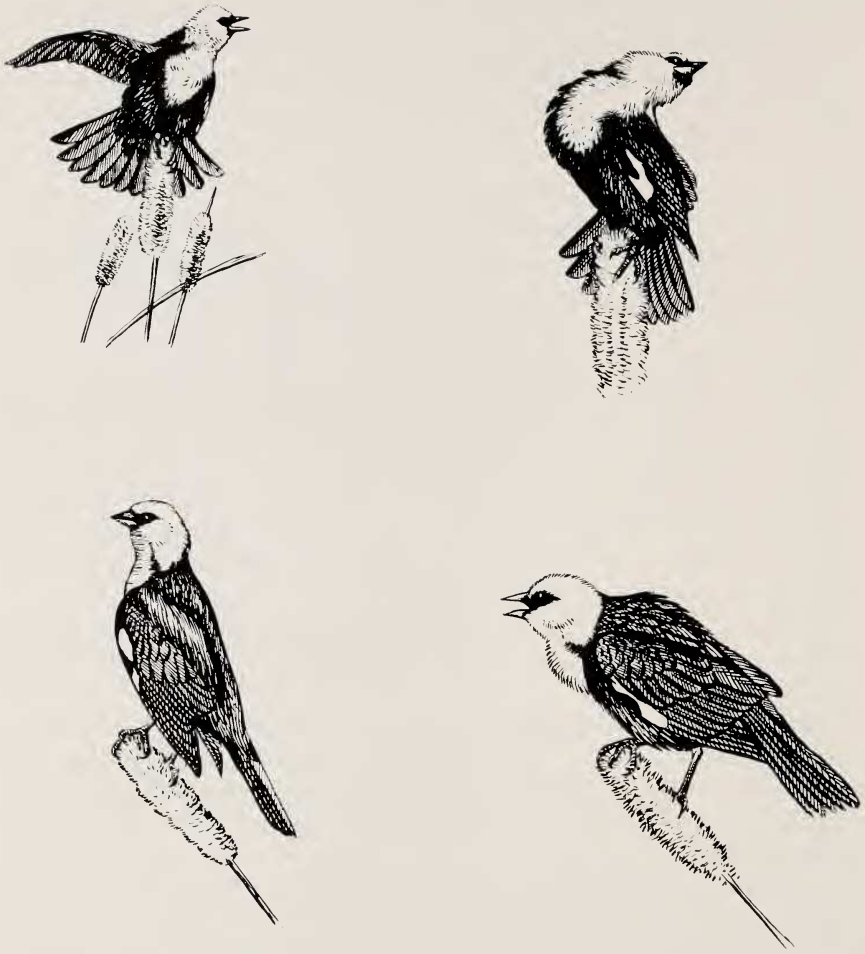

FIG. 1. Song-spread display, male Yellowhead (above); alarm posture (lower left); and "hawk call" posture (lower right).

sis) (two), Marsh Hawks (*Circus cyaneus*) (five), and a Short-eared Owl (*Asio flammeus*) (one). The "hawk call" was given in each case (by many birds), but only the owl was chased. Often the call was given while perched, but occasionally males flew up into the air and circled, as described by Linsdale (1938:133). Once the call was given by several males to a low-flying crow, then one male flew up in hovering flight beneath the crow, giving the full call. On another occasion males gave the soft *prill* notes while out of sight as a Red-tailed Hawk soared high overhead. Good reactions were obtained experimentally by placing a mounted female Marsh Hawk in a male's

territory in his absence. Nearby birds gave the *clerrk* call, but when the territory owner suddenly returned, he at once gave the full "hawk call" while circling overhead. Once I saw a female Yellowhead dive into the cattails as a Marsh Hawk flew over. A male I was watching at a feeding place off the marsh showed an immediate alarm reaction when the "hawk call" was given by birds on the marsh. He stopped moving, held his head high with bill straight ahead and feathers compressed, and, with feathers on the back of the head and neck erected, he remained in this tense alarm posture for several seconds afterwards (Fig. 1). Wetmore (loc. cit.) reported that distant feeding males returned to the marsh when birds on the territory gave this call. I noticed a male once clearly give this call as it arose from a field, heading toward its far-distant territory. In this situation the call seemed related to the aggressive "flight-song" of the Red-winged Blackbird (Nero, 1956:10–12), which seems to have no counterpart in the Yellowhead. Chapman (1930: 355, 370) describes a "rapid cackling alarm note" for the Wagler or Chestnut-headed Oropendola (*Zarhynchus wagleri*), which appears to be related to this alarm call of the Yellowhead.

(4) Female scolding or alarm calls: These are of two main types: harsh, short, and repetitive *yah-yah-yah*, and high-pitched, reedy, and screeching sounds. (When chasing females in sexual chase males occasionally uttered a series of similar, loud, harsh notes.) Females also frequently called *wheesh-wheesh* when leaving the territories to go to feed.

Precopulation and copulation calls.—Both sexes have a low, soft, rapid, and repetitive or trilled call (*pree-pree-pree . . .*) which is often given continuously during precopulation and copulation. This was heard in the male chiefly during copulation; once it was accompanied by a noticeable vibration of the throat feathers. A similar call is given by the Redwing (Nero, 1956: 32).

AGONISTIC BEHAVIOR

Male Song-spread.—Song-spread is a term which has been applied to the combination of primary song and plumage display of the Redwing. (The term is comparable to "ruff-out" as used by others for other icterids.) A similar and homologous display is given by the Yellowhead (Fig. 1). As in the Redwing, the form of the Song-spread given by the Yellowhead is variable, from a short or weak version of the song with little plumage display, to the extreme song and posture. Usually the tail is down and spread, the plumage of the back and throat is erect, and the wings are held out to some extent. Just as the wings are sometimes kept out after the close of song, they may be sometimes returned before the song ends. Song is invariably accompanied by some erection of the yellow feathers, at least, and usually by a fluffing or erection of most of the body plumage. Whatever the extent of

song, it is usually preceded or accompanied by a lowering and spreading of tail feathers.

The display is invariably asymmetrical, the right wing nearly always being held out either alone or to a greater extent than the left one, and the head and neck being turned far to the left, so that the bird sings over its left shoulder. This peculiar habit was noted previously by Linsdale (1938:132), Ammann (*in* Bent, 1958:117), Roberts (1936:299), and Fautin (1940:79). During Song-spread the wings may be held below, at, or above body level, but in extreme display the wings, especially the right one, are held upward, usually highest at the climax of song. They may be held up briefly after the close of song.

Song-spread may be given in the absence of other birds but it is usually directed toward one or more birds, and especially in response to the song of others. Song is elicited by intruding males, neighboring males, new males and females, and even the mate. As in the Redwing, it may be given alternately with other agonistic displays in territorial encounters. It appears most extreme when directed toward birds flying over the territory, especially females.

Frequently both wings are displayed to such birds in a combination of Song-spread and Elevated-wings (see Courtship below). The response to males and females flying slowly overhead often appears to be similar. A similar situation has been reported for the Redwing (Nero, 1956:131). It may be that the birds flying slowly overhead are seeking territories or "challenging" (Nero, 1956:134), or appear to be, thereby eliciting more extreme display.

Song may also be given with the full-stretch posture (neck to full length) without any spreading of the wings. Since Song-spread often is given during territorial disputes and since it often precedes attack it may be considered to function mainly in a warning or threat sense, but, as in most birds, it apparently also functions to attract females. Certainly, it draws attention to the displaying bird.

Female Song-spread.—Female song is relatively simple and usually is given from an upright position. As in the male, it is accompanied by varying degrees of plumage display; in its extreme aspects it approaches the full Song-spread of the male, but the song is rather limited. Females in full Song-spread apparently also sing over their left shoulders. Song-spread is given almost always to other females, either flying overhead or intruding on the home territory, and it often precedes fighting. It is far less frequent than male display and evidently is less common and more specifically directed to other birds than is Song-spread in the female Redwing. Nevertheless, female Yellowheads are equally belligerent and often are involved in agonistic be-

havior with other females. Several extreme Song-spreads were given to nearby females by a highly disturbed female whose nest had just been "robbed."

Male Song-spread in the Icteridae.—Song-spread display, in which the male emits a brief song accompanied by some plumage display, appears to be homologous in many icterids. Hudson (1892:273) states: "In the Troupials . . . there are many that accompany singing with pretty or grotesque antics." The Song-spread of the Redwing, the Yellowhead, and Brewer's Blackbird (*Euphagus cyanocephalus*) (the "ruff-out," Williams, 1952:5), for example, appear to be basically similar. Lanyon (1957:32) suggests that "expansion posturing" of the meadowlarks is similarly related. A corresponding relationship appears to be evident among several other icterids, namely the Tricolored Blackbird (*Agelaius tricolor*) (Lack and Emlen, 1939); Rusty Blackbird (*Euphagus carolinus*) (pers. obs.); Great-tailed Grackle (*Cassidix major*), Boat-tailed Grackle (*C. mexicanus*), and Common Grackle (*Quiscalus quiscula*) (Bent, 1958; Selander and Giller, 1961; Skutch, 1954), Shiny Cowbird (*Molothrus bonariensis*), Screaming Cowbird (*M. rufo-axillaris*), and Brown-headed Cowbird (*M. ater*) (Friedmann, 1929); the Yellow-rumped Cacique (*Cacicus cela*), Montezuma Oropendola (*Gymnostinops montezuma*) (Skutch, 1954); Wagler Oropendola (Chapman, 1928); and probably others. Most characteristically, the tail is lowered and spread, the wings are held out to some extent, and various parts of the plumage are erected, the contour plumage being fluffed in many.

Although different parts of the plumage are apparently displayed prominently by different species, e.g., humerals in Redwings, scapulars and rump feathers in Brewer's Blackbird, neck feathers in Common Grackle, flanks in Wagler Oropendola, etc., a comparative study will require very careful examination of these relationships. We tend to note especially the erection of the colored parts of the plumage and overlook less noticeable parts which may, however, be significant in tracing relationships. If a comparative behavior study is ever to be made of the Icteridae, as has been done for the Anatidae (Delacour and Mayr, 1945), a more detailed analysis of Song-spread (and other displays) than has been made will be necessary. Note, for example, that Redwings in Song-spread (see Nero, 1956:11) erect or fluff-out nearly all parts of their plumage; the red secondary wing coverts are most noticeable and attract our attention, but if other parts, say the nape or rump feathers, were conspicuously colored, then these would also be given special mention. We also tend to see in the erection of colored plumage an explanation of its function and origin, but this may not necessarily be so. For example, although the cream-colored nape feathers of the Bobolink (*Dolichonyx oryzivorus*) are erected and obvious in Song-spread display, they may have a more significant function and may have evolved in relation to another display, such as Nodding (see beyond). I think, on this basis, that we shall have to be cautious in our assessment of the relationship of plumage and behavior.

Female Song-spread in the Icteridae.—Song in female birds is relatively uncommon (Nice, 1943:131) but it has been reported for a number of icterids in which it is accompanied by plumage display; it appears homologous to Song-spread of the male. Skutch (1954:335), in a summary of the Icteridae, states: "In many tropical species the female has a well developed song but does not quite equal the male in richness of voice." Female song or Song-spread has been observed or reported for the Redwing (Proctor, 1897; Dubois, *in* Bent, 1958:141; Nero, 1956:10), Common Grackle (Eyer, 1954: 47), Brewer's Blackbird (Williams, 1952:5), Bullock's Oriole (*Icterus bullockii*) (Miller, 1931), Rusty Blackbird (pers. obs.), Boat-tailed Grackle (Robert K. Selander, pers.

corresp.), and others. It appears chiefly in agonistic encounters with other females. In polygynous species, e.g., the Red-winged and Yellow-headed Blackbirds, females defend an area around their nest against other females; in the monogamous Bullock's Oriole the female shares in the defense of the male's territory, but her hostility is still directed toward other females (Miller, op. cit.).

A female Rusty Blackbird, when disturbed at her nest, repeatedly gave song (like that of the male) when confronting the observer, the less aggressive male of the pair usually remaining at some distance and in relative silence (pers. obs.). This suggests a hostile function for song in this species. Selander (pers. corresp.) notes a further function of female song:

"In Brewer's Blackbird (Williams, 1952) and in the Common Grackle, mutual Song-spread of male and female is a very conspicuous part of the early stages of pair-formation. In these species the female is not dominated by the male, with the result that male and female behave much as do two males confronting one another. In the Boat-tailed Grackle, on the other hand, females are at all times and in all places completely dominated by the much larger male. There is no possibility of her contesting with a male of nearly twice her mass (the degree of sexual dimorphism is, of course, related to the mating type). In a sense then, she has no need for the Song-spread to indicate her "resentment" at the approach of a male—she merely flees. There is no long period of mutual display in *Cassidix* as there is in *Euphagus*, since there is no pair-bond formed.

"In the Great-tailed Grackle the male is not quite so completely dominant over the female, and, in correlation, Song-spread is occasionally directed to the male.

"In sum, I would say that female Song-spread, like male Song-spread, has threat function, but the degree of importance it may have in female-to-male relationships depends on the particular dominance relationship existing between the sexes. In some species it apparently has a very important function in pair formation; in other species it has none."

Bill-tilting and Flight Bill-tilting.—A characteristic agonistic display in the Redwing and many other icterids is a posture in which the head is raised with the bill tilted upward, a position which may be held for several seconds. This has been variously termed Head-up, Pointing, Bill-tilting, etc. In the Redwing it is usually given in agonistic situations between males, and between females. It is given while perched or standing, usually in silence and with the plumage compressed (in strong contrast to the erect plumage in Song-spread displays). It is given most frequently, and often alternately with Song-spread, by disputing males on territory boundaries (Nero, 1956).

In the Yellowhead, Bill-tilting while perched is seen only rarely, but it is replaced by Flight Bill-tilting which is believed to be homologous (Fig. 2). For example: it is given most often by aggressor birds in the course of driving an intruder from the territory; when dummy males (stuffed birds) were offered to territorial males, on their territories, Flight Bill-tilting invariably preceded actual attack.

Flight Bill-tilting has been reported previously for the Yellowhead by Ammann (quoted *in* Bent, 1958:103): "'He proceeds toward the female in one or more short, jerky flights—thus causing the wings to beat very loudly, with bill pointing almost straight up.'" (I am inclined to believe that this

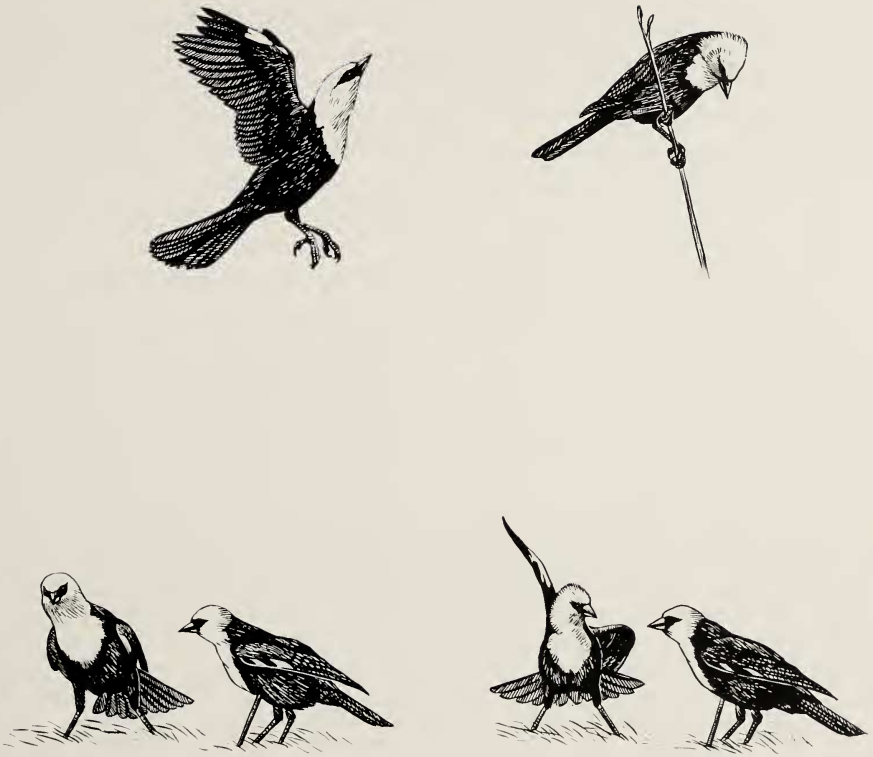

FIG. 2. Flight Bill-tilting (upper left); Nodding (upper right); agonistic behavior to dummy (below).

display, although given in the presence of the female in this observation, was probably directed toward neighboring males.) Linsdale (1938:133) also noted this display as follows: Two males disputing along a territorial boundary ". . . made short flights, getting scarcely more than a foot above the ground and moving, altogether, only 3 or 4 feet. Once one went as far as 10 feet. In these flights the wings were flapped violently, but the bird moved slowly, and the body was held with the bill pointing upward 80° above the horizontal."

In Flight Bill-tilting a bird flies toward an opponent with slow, flapping flight and as it approaches the second bird it rises upward with full strokes and momentarily closes its wings, and with its head and neck thrust upward to full length, until its body is nearly vertical. At this moment forward movement is nearly halted and flight is noticeably labored. A moment later the bird drops to a perch and at once assumes a different posture, e.g., Nodding (beyond). While flying, its feet hang down loosely and the tail may be raised

occasionally as if for balance. During a dispute both birds may change perches several times, drawing closer to each other, or, as one moves away, the aggressor, or both birds, may give Flight Bill-tilting in the short flight to a new perch. When making a long flight toward an opponent (or a dummy) Flight Bill-tilting was not given until the bird had approached to within several yards or feet. While usually given to other males, on one occasion a male so displayed to his mate, and at another time a male gave this display to a neighboring female which was scolding on the adjacent territory.

Flight Bill-tilting is also given by females to other females in much the same way and in the same situations as described for the male. Bill-tilting (while perched) has been observed occasionally in females (given to intruding females). On two occasions a female gave Bill-tilting while walking toward another female which was then driven off. Wetmore (1920:403) describes a male Brown-headed Cowbird running while giving Bill-tilting, and I also have seen this.

A kind of Flight Bill-tilting was suggested for the Redwing (Nero, 1956:134) in which intruding males while in flight over a territory abruptly tipped their bills upward, and on 15 May 1958 (at Regina), a male was definitely seen giving Flight Bill-tilting while engaged in a territorial encounter with its neighbor. However, it is comparatively rare in this species. Flight Bill-tilting evidently occurs in the Eastern Meadowlark (*Sturnella magna*); Saunders (*in* Bent, 1958:58) reports on three males that were competing for the attentions of a female, thus: "The males vied in following her, first one then another arching his body, pointing his bill up, and flying jerkily toward her at an elevation of from 3 to 6 feet." Lanyon's description of "jump-flights" in meadowlarks (1957:32) appears to represent the same behavior.

On 3 May 1960, at Regina, Bill-tilting and Flight Bill-tilting were elicited from a male Western Meadowlark (*Sturnella neglecta*) during attempts to record the unusual vocalization of this bird. A well-mounted male Western Meadowlark with bill somewhat elevated was placed on the ground near the bird. It responded with extreme Bill-tilting, tail-flashing, and small "jump-flights" (with Flight Bill-tilting) over the dummy. No song was given. Finally, it attacked the dummy, pecking at its head (but its behavior also resembled copulation). At times it had held its bill upright in Bill-tilting for extended periods of several seconds.

Flight Bill-tilting has also been described for the Brown-headed Cowbird: "At once a second male came flying in, and, suddenly checking when two or three feet from the bush, extended the bill straight up and in this attitude came down slowly to a perch three feet from the first bird" (Wetmore, 1920:402). On 15 June 1958 (Emma Lake, Saskatchewan), a group of male cowbirds contesting over a few females in a tree were seen giving this display between courtship displays (Song-spread and Bowing). It was regularly given by each male as it flew toward another to displace it from its perch. On 2 June 1958, at Regina, several males, when following and courting a female which was feeding and rapidly moving along on the ground, regularly gave short hop-flights and Flight Bill-tilting. Selander states (pers. corresp.) that Flight Bill-tilting is common in this species.

It may be misleading to consider Bill-tilting and Flight Bill-tilting together

since they may have slightly different functions. However, no such differences are apparent. The hostile or agonistic aspects of "tilting" are quite clear and in a general sense tilting may be termed threat display. Both kinds of tilting, for example, invariably occur with other hostile displays (in the Yellowhead: Song-spread, Crouch-bristling, Nodding, and actual attack). Frequently, attack immediately follows tilting, with no noticeable change of attitude. This all suggests that tilting is indeed a threat display ". . . 'designed' to intimidate an opponent, to make the opponent retreat or flee" (Moynihan, 1955*b*:256). Tilting may be related in origin to a similar attitude seen in the Jackdaw (*Corvus monedula*) where ". . . the rivals threaten each other by drawing themselves up to their full height [with beaks up] and flattening their feathers. This attitude implies the intention of flying upwards and onto the back of the adversary" (Lorenz, 1952:165). Sleeking of the head and neck feathers, which is a common aspect of Bill-tilting and Flight Bill-tilting, is interpreted by Marler (1956:60) as a flight intention movement in the Chaffinch. In the Yellow-headed Blackbird and other icterids, sleeking may have been derived from an intention movement to fly, but it seems likely that its functional significance lies in the emphasis it gives to the bill.

Other aspects of tilting suggest that it may function as an appeasement display in the sense used by Moynihan (op. cit.:257): ". . . 'designed' to prevent attack by directly reducing the actual and relative strength of an opponent's attack drive, without provoking escape by the opponent or any general reaction by neighbors and companions." For example, tilting does not necessarily precede attack; it is sometimes given by a bird moving away from its opponent, and it is most frequent and protracted in bouts between adjacent males on territory boundaries. Moreover, in the Yellowhead, territorial encounters are also often accompanied by Tail-lifting display (below), which is considered to have an appeasement function. Withdrawal tendencies are also apparent, especially in the Redwing where tilting is sometimes given laterally or with averted posture. It seems to me that tilting may have arisen out of escape/attack conflict, the display (extended neck, upright bill, and compressed plumage) representing strong escape tendencies. Regardless of origin of the display, its function seems clearly to be hostile, whether in a direct threat sense or as appeasement. Further study of the display in these and other species will be needed in order to clarify its origin and function.

There are some differences between Bill-tilting in the Redwing and Flight Bill-tilting in the Yellowhead, in addition to the obvious aspect of motion, although these differences are related to this aspect. In the Yellowhead, the display is given by only one bird at a time, whereas in the Redwing frequently it is nearly mutual; the display of the Yellowhead is very brief, compared to the several-seconds-long display of the Redwing; and it is usually given while

advancing, not while maintaining a rather definite position. There may be some significance to these differences as related to territorial defense and aggressive tendencies, but I am unable to see this. Perhaps the main point here is that we are looking at displays which have been similarly derived and which have similar functions but which represent different levels of development and ritualization. I think that the Yellowhead Flight Bill-tilting is the more primitive display.

Alternation of Song-spread and Bill-tilting has been described in the Nicaraguan Grackle (*Cassidix nicaraguensis*) by Belt (1874:214), who notes in particular the contrast between the fluffed plumage of Song-spread and the compressed plumage of Bill-tilting; he adds: ". . . its sudden change in appearance after delivering its cry was ludicrous. It appeared as if it was ashamed of what it had done, and was trying to look as if it had not done it—just as I have seen a schoolboy throw a snowball, and then stand rigidly looking another way." Armstrong (1947:251) comments on the Bill-tilting display of the Nicaraguan Grackle (and other birds) as follows: "The connexion between static posturing and dark plumage deserves investigation. The colour black has a strong emotional valency and is common as a psychological weapon. Also, to stand perfectly still is one of the most surprising things such a volatile creature as a bird can do." The ritualized nature of Bill-tilting in the Icteridae, which apparently occurs most frequently in the blackest ones, may be related to these factors.

"Courtship behavior" in the meadowlarks apparently involves Bill-tilting. Saunders (quoted by Bent, 1958:58–59), for example, states that in the "usual courtship display" the male Eastern Meadowlark "'. . . raises his body to its full height, stretches his neck to its full length, and points his bill to the zenith . . . the female's reaction to this performance is to raise her body to its full height, stretch her neck, and point her bill. . . .'" Lanyon (1957:39) describes different behavior which fits the general pattern. It would appear that Bill-tilting occurs more often between male and female meadowlarks than in pairs of either Redwings or Yellowheads. One wonders whether this apparent stronger aggressive behavior on the part of the female meadowlark to males is related to the nearly similar size of male and female in this species and to possibly their strong similarity in color and form. Selander points out, e.g., that such aggressive behavior never occurs in *Cassidix*; the female being completely dominated at all times by the male (pers. corresp.).

Nodding.—Nodding is a deliberate downward movement of the head which often appears in agonistic situations. In Nodding, the neck is arched so that the bill points down (Fig. 2). It varies from merely a slight arching of the neck and downward-directed bill to an obvious lowering of the head with the bill nearly touching the feet; it is usually held only momentarily, though it may be repeated often. When giving this display on the ground the tarsi are flexed slightly so that the body is lowered. Erection of the back feathers coincides with or reinforces Nodding. Usually the head is not lowered below body level; often the body is held more or less erect. It is often given by disputing males on the territory boundaries where it may precede or follow Flight Bill-tilting (see above), and it may be given during aggressive repul-

sion of an intruder. It is often given in between Song-spread displays. It is invariably directed toward (or nearly toward) an opponent or stimulus source. Since observing Nodding in the Yellow-headed Blackbird I have noted its occurrence in the Red-winged Blackbird, but it evidently occurs less frequently in this species. I suspect that there is some relationship between Nodding and Bill-wiping. The latter display occurs frequently in agonistic situations in both the Brown-headed Cowbird and Red-winged Blackbird, and is possibly less common in the Yellowhead. According to Selander (pers. corresp.), in *Molothrus ater* Nodding is an intention movement to Bill-wipe. Although Nodding has not been seen in female Yellowheads it may be mainly because there have been fewer observations of female/female conflicts. On one occasion a female was observed giving an aggressive "song"—evidently to another female—a harsh, nasal *rahh-rahh* and *rahh-rahh-rahh*—while on the ground in a horizontal position with head lowered and bill pointing down. This was also given while the female was perched on cattails. The posture appeared to be related to Nodding.

Nodding also seems to have some relationship to a display involving the nape feathers reported for the Bobolink. In one case a male, perched on a fence near a female which was giving distraction display on the ground, several times gave "a sudden deep bowing movement in which the fully erected, buff-colored nape feathers were directed down toward the female. This bowing posture was held for some time even after the female had moved quite far ahead of the male. The significance of the male's display at this time was not clearly apparent . . ." (Nero, 1955:34). Townsend (quoted by Bent, 1958:33), in speaking of the courtship display of the Bobolink, says: "He erects his buff nape feathers, points his bill downward. . . ." It seems possible that Nodding is a well-developed display in the Bobolink, although this needs to be verified, and that the conspicuous nape feathers are related to this particular display.

Possibly related behavior has been observed in some other icterids. Chapman reports (1928:154) that once when a female Giant Cowbird or Rice Grackle (*Scaphidura oryzivorus*) (see Parkes, 1954, regarding generic name) attempted to enter a nest of a Wagler or Chestnut-headed Oropendola and confronted the female oropendola, she held her bill down then curled her head downward until her bill touched the lower breast. This observation seems related to recent studies of apparent appeasement behavior in the Brown-headed Cowbird (Selander and LaRue, 1961). Male and female cowbirds in captivity persistently approached other species and Nodded, presenting their nape with erect plumage. Preening of the cowbird's nape feathers by the other bird was the surprising response and this was interpreted as an appeasement situation, which, in the wild, would be of advantage to female cowbirds when intruding on foreign territories.

Selander (pers. corresp.) states: "The nod as such probably has some value in appeasement by concealing the bill from direct view of the opponent and by averting the eyes (it is also opposite of the bill-tilt). I wish I knew what its evolutionary connection with other nodding behavior was. E.g., the male Red-eyed Cowbird [*Tangavius aeneus*] makes a very conspicuous nod before the female as he is courting. This is most interesting: he is before the female, hopping toward her with quivering wings and erect plumage; suddenly the wings stop and for one-half to one second he holds the nod—and his cape is well displayed. Then he begins to quiver the wings again. Then he may stop and

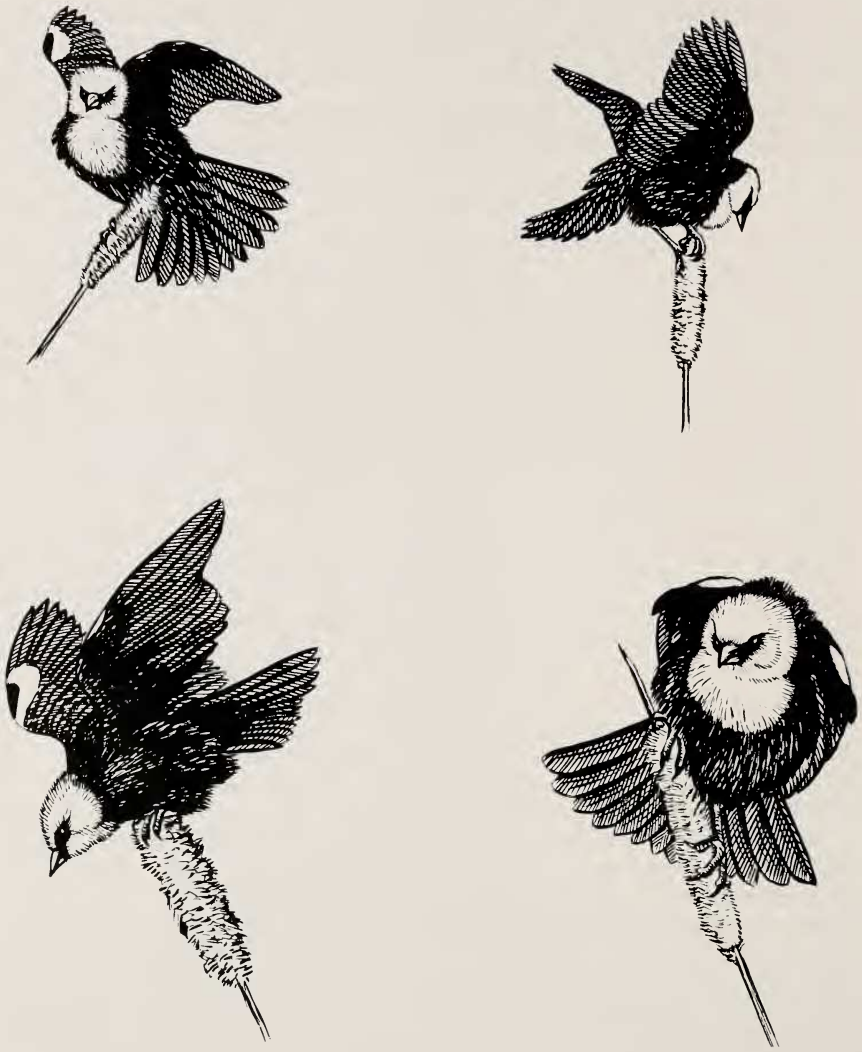

FIG. 3. Courtship display--Elevated-wings and Bowing (above; lower left); precopulatory display—Crouch-bristling (lower right).

nod. Of course this nodding and that of *Molothrus* and your birds is very similar structurally to the prolonged preening invitation dispaly of *Molothrus* and *Tangavius*. About all I can say is that in every case in which it has been seen the nod has appeasement function. The parasitic cowbird 'wishes' to appease some other species in order to approach and induce preening, and the Yellowhead presumably reduces the attack or escape 'drive,' of an opponent by nodding. This same sort of display or posture occurs in a great variety of other birds from eagles to parakeets."

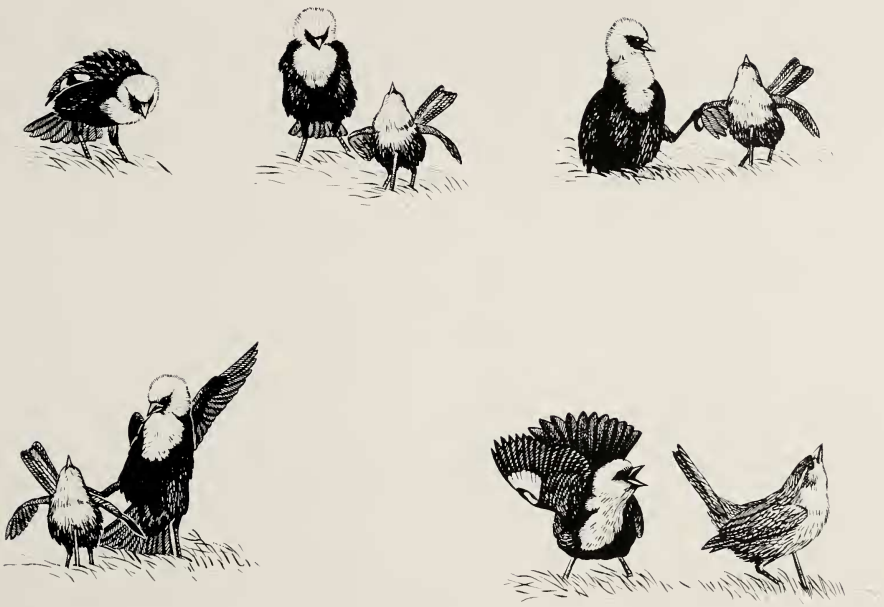

FIG. 4. Precopulatory behavior to a female dummy—first phase (upper left), showing Crouch-bristling; second phase (upper middle, right, and lower left); Song-spread display to dummy (lower right).

Crouch-bristling.—This term may be used to describe a crouched and hunched posture in which the plumage of the upper back, breast, and head is fully erected; the tail is fully spread and lowered and the wings are held out somewhat (Fig. 3). The displaying bird faces its opponent with its head held low and parallel with or lowered beneath the body level, but with the bill forward. The yellow plumage on the top and back of the head is noticeably erected which, together with the black pattern of the lores, etc., gives strong emphasis to the bill. Crouch-bristling is regularly given in agonistic situations where it appears to have a threat function. A very similar if not identical display is also addressed to the female in general sexual situations and in precopulation (Fig. 4, first phase). The occurrence of such a display in sexual situations still appears to be agonistic in nature. Crouch-bristling is clearly related to "crouching" in the Redwing (Nero, 1956:17), as well as the "peck-gesture" as defined by Laskey (1950:159) for the Brown-headed Cowbird. The "threat-posture" of the Song Sparrow (*Melospiza melodia*) is similar (Nice, 1943:156), as is the "'head-forward' display" and the "'crouching' posture" described by Marler (1956:37, 103) for the Chaffinch; the former display functions in fighting, the latter in courtship. Marler's observations are more detailed than ours and a complete comparison cannot be

made. However, his material serves as a useful guide in explaining Yellowhead behavior. " 'Head-forward' display is always associated with an obvious intention to attack which is checked, it seems, by a conflicting tendency to escape" (Marler, 1956:39). The " 'crouching' . . . display is similar to an extreme form of the 'head-forward' posture. . . ." In the " 'crouching' posture" both aggressive and escape tendencies appear to be active, while a copulatory tendency is not yet in evidence (Marler, 1956:103, 105). (This is discussed further under Precopulation.) I am unable to differentiate between Crouch-bristling as it appears in agonistic and sexual or courtship situations in the Yellowhead; however, my observations are far from complete. In a filmed sequence of a male confronting and then attacking a male dummy, the initial behavior with compressed plumage, wings out and frequent withdrawals, suggests strong escape tendencies. At one time the bird gave Crouch-bristling, appeared more confident, and showed less escape tendency and more approach or attack tendency. He soon attacked the dummy, knocking it over, and then went into Tail-lifting display (discussed below).

Crouch-bristling usually is given prior to supplanting an intruder. On the open ground this often takes the form of an aggressive though somewhat indirect, rapid, sidling gait, or "shouldering." This may be succeeded by an even more aggressive action (actually attack behavior)—the "direct-run," with head down, bill forward and sometimes open, etc., straight and fast toward an opponent. The "direct-run" usually displaces an intruder and is probably comparable to the "direct-flight" which routs an intruder perched on the cattails.

A filmed sequence of a female attacking a female dummy shows a behavior similar to that of the male, including shouldering, tail down and spread, head sometimes hunched, feathers on top of head flattened and level with back, bill forward, wings out from the body and at times partly lifted over the back, and primaries at times touching the ground. Crouch-bristling occurs but is less noticeable, although nearly all feathers of the body are involved, including the wing coverts. In actual attack the female landed on the dummy; squatting on her tarsi and braced with her tail she pecked at the head of the dummy. The posture somewhat resembled copulatory behavior. More complete apparent copulatory behavior in an agonistic situation was given by a female Baltimore Oriole (*Icterus galbula*) to a female dummy in brief experiments made in June of 1958 by Richard W. Fyfe (pers. commun.). A mounted female oriole was placed on a lawn in precopulatory pose (tail and head up, wings partly out) where a pair of orioles were frequent visitors. Both male and female attacked the dummy. The more aggressive female approached the dummy giving the alarm *chirr* and Open-bill, then attacked the dummy by standing on top of it and pecking at the head (and cloacal region?); several times the female went through exact motions of copulation (judging by Fyfe's photos), as did the male, including lowered tail, squatting on tarsi, and wing fanning. Redwing males, in addition to often attacking male dummies, frequently also attempted to copulate with them in experiments performed by myself and others. The subject of males' copu-

lating with dummies is discussed by Nice (1943:206–208); however, I found no mention of attempted copulation (or similar behavior) by a female bird to a female dummy. Selander (pers. corresp.) states: "Females of *Cassidix* regularly mount female dummies and perform the complete masculine copulatory pattern. Here there is no conflict between tendencies, only a simple 'release' of the pattern by the dummy. I have a good idea as to why this occurs only in *Cassidix*, not in *Euphagus* and the rest. In those species other females are potential rivals and there is a premium on female territoriality and associated aggressive reactions to the close approach of other females. In the promiscuous *Cassidix*, on the other hand, there is no rivalry for males, and in a sense, the masculine pattern is not inhibited by other tendencies. Thus, when a female sees a female dummy, the masculine pattern is stimulated and is free to express itself. Also, since the masculine pattern is unusually strong in males of promiscuous species (a male *Cassidix* will mount a dummy fifty or more times in a row), perhaps it is also unusually strong in the female."

Tail-flipping.—Tail-flipping is a common display and seems to indicate general nervousness or alarm. It consists of a quick flip of the tail: the tail is lowered, spread, closed, and returned, all in one quick movement. It is given by both sexes and is alike in Yellowhead and Redwing. Marler (1956:157) described Tail-flipping in the Chaffinch, and considered it a flight-intention movement. This display is more noticeable in the meadowlarks where it is reinforced by a conspicuous white tail pattern and where it may have greater significance. However, flashing of the black tail of Yellowheads and Redwings is surprisingly conspicuous when viewed against the skyline or the marsh vegetation which is their usual habitat.

Tail-lifting.—As indicated by Ridgway (1902:347), the female Yellowhead has a yellowish anal tuft (or circlet), the male, yellowish or orange feathers in the anal region. In a recent examination of several specimens it was determined that both sexes have a colored anal circlet, and that in the male there is in addition a prominent colored patch involving the feathers immediately posterior to the anal circlet and including the basal portions of some of the under tail coverts. There is considerable individual variation in the extent of this patch. The yellow cloacal patch of feathers (including the anal circlet) is evidently related to a display in which the tail is raised or lifted, though not usually spread, thus revealing the cloacal area. This display has been termed Tail-lifting. In display the tail is raised from just above the horizontal to a nearly vertical position, depending upon the situation and presumably the motivation, and held briefly, for several seconds or for a few minutes (Fig. 5). The plumage is usually compressed and the head may be held high. It appears in moments of contest or conflict between males, between females, and between male and female. It is more prominent in the male. In a few cases it appeared to be given in flight in agonistic situations, especially in connection with Flight Bill-tilting. At low intensity Tail-lifting is often given from fortuitous positions, but in high-intensity displays the bird

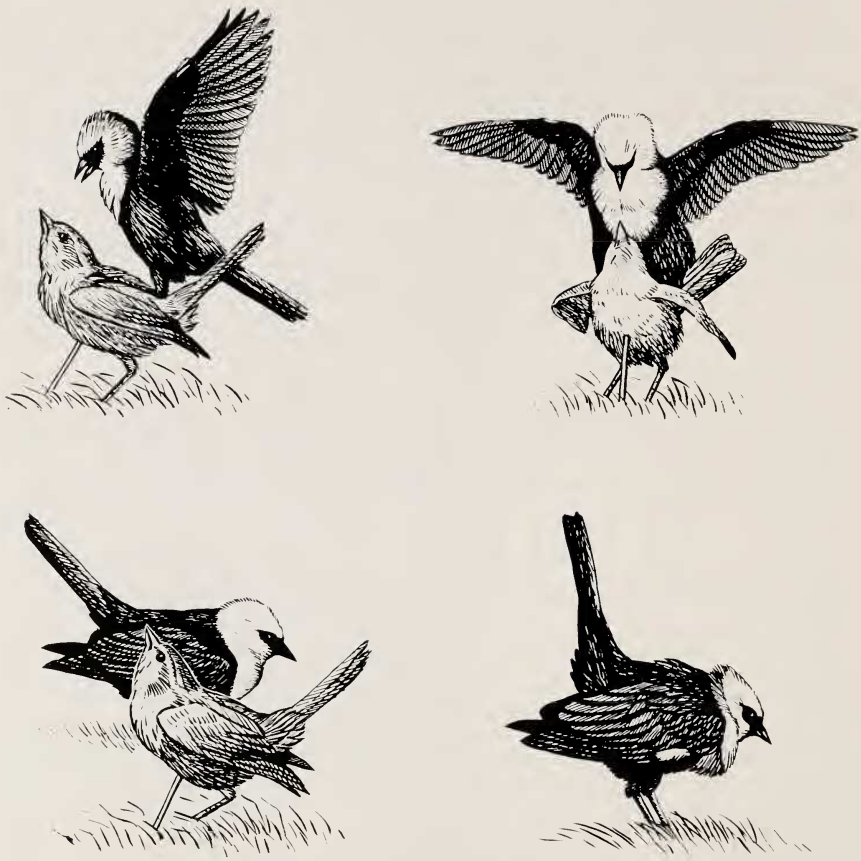

FIG. 5. Copulatory behavior to a dummy (above); Tail-lifting display to dummy (below).

faces away from its opponent, thus fully displaying the cloacal region. This display may be related to, and may stem from, precopulatory display of the female (or the appeasement aspect of this—see below) since other elements of this latter display also appear, e.g., slightly spread primaries. Moreover, in the female an apparently advanced form, similar to female precopulatory display, is given in much the same way. It has occurred to me that the origin of the colored cloacal patch in the Yellow-headed Blackbird, and its relationship as a part of an appeasement display, may be related to the protruding cloaca of the female in extreme precopulatory display. In both sexes, Tail-lifting apparently functions as appeasement. Still, the more aggressive Tail-lifting member may Tail-lift first. The following field notes serve to illustrate typical situations:

16 May 1958, 7:00 AM: Two Yellowhead males, one holds its tail up and its primaries out from its body exposing the cloacal patch; performed this rather deliberately three to five times with its posterior toward the other male. They move about on the cattails, keeping together, with Bowing, Crouching, and Song-spread in between. These two are newly engaged in contest; one is contesting for space with an already established male. They maneuver back and forth on the territory edge (newly formed). Later one drives off the other.

19 May 1958, 7:00 AM: Two males on territory border, both with tails up and reversed momentarily as they first meet. They move with Flight Bill-tilting and again one (highest position) elevates tail while facing away.

20 May 1958, 8:11 AM: Male in noisy flap flight for three feet—by his female but also near adjacent male on territory border. First male holds tail up sideways as the males meet and move apart.

27 May 1958, 8:10 AM: Female resting on water pipe in strange territory, as a male approaches her she lifts her tail, then flies away.

8:36 AM: Female in Tail-lifting to another female; as her mate approaches she maintains the Tail-lift and gradually shows precopulatory behavior, but the male is only aggressive and attacks her.

9:00 AM: A female very aggressive to a neighboring female with Flight Bill-tilting and Song-spread, then actual attack; at attack the other female goes into Tail-lifting (or a facsimile of precopulatory display), at which the mate (of both these females) approaches and attacks the aggressor female.

10:00 AM: Two females fight, one puts tail up and gives wing flutter (much like precopulatory display), but the male is not nearby.

An interesting Tail-lifting display which provided additional features was given repeatedly by a male involved in behavior to a female dummy on 3 June 1958. A complicated sequence of events, lasting 5–8 minutes, including Song-spread, Precopulation, and Copulation, and alternating with Tail-lifting was repeated several times during the course of half an hour and was filmed (Figs. 4, 5). Following each copulatory phase the male suddenly underwent a surprising transformation from a very active state to a nearly rigid and transfixed behavior in which Tail-lifting predominated.

A typical sequence: the male walks around the dummy to face it, sometimes being sideways to it, with his tail lifted part way and with a few deliberate Nods. Holding his wings out loosely he stops, moves mechanically, braces his feet, cocks his tail higher and higher, while emitting a kind of clicking sound, until his tail is straight up. Then suddenly he swings about to fully face away from the dummy. After a few minutes of this behavior the male suddenly breaks into Song-spread and then rapidly goes into precopulatory behavior. It appears that there was some conflict between sexual and agonistic behavior in this situation. Under usual circumstances Tail-lifting, apparently functioning as appeasement, may arise out of conflict. In a filmed sequence in which a male Yellowhead attacked a male dummy, Tail-lifting was given with the tail spread rather fully. Initially the male kept his plumage sleeked, his wings out, his tail fully spread, and generally appeared very wary (Fig. 2). Finally, as he "gained confidence," he fluffed his plumage, crouched low, and then knocked the dummy over. Tail-lifting then occurred, the spread tail being raised gradually as the male turned from the dummy; he stopped, facing directly away from the dummy, with the spread tail held nearly vertical.

Tail-lifting occurs normally in one other common situation. Males feeding together on the ground often walk about with their tails up. This is also common in Redwings (Nero, 1956:13), cowbirds, and possibly other icterids. Bent (1958:444) writes of the Brown-headed Cowbird: "While feeding it often holds its tail erected high in the air, with the wings drooping below it." Nichols (1960) illustrates a cowbird using "tail-up posture while feeding." And he states: "Tentatively, I interpret the protracted tail-up silent foraging of the cowbird as a rudimentary and fractional display indicating emotions which, when reaching full development, will give rise to complex tail-up displays with invitation application." It is possibly appeasement behavior here too, where males in close association show some agonistic behavior. In the Redwing when a male is feeding together with other males on the ground, the red coverts are usually kept concealed (Nero, 1956:9), behavior which indicates an appeasement or nonaggressive situation. Tail-lifting is not otherwise common in the Redwing. I have seen Redwing males lift their tails high on only a few other occasions. In one case a male, perched on a fence-post and greatly disturbed at my presence on its territory, gave alarm cries while holding its tail high.

In the Brewer's Blackbird there is an "elevated tail display" (with tail somewhat spread), which may be related although "it is never addressed to another male and has no significance as a threat . . ." (Williams, 1952:7–8). Since there is no cloacal patch (of colored feathers) in either the Redwing, Brewer's Blackbird, or cowbird, it may be that this display has not developed to the same extent in these species as in the Yellow-head, although clearly functioning at a low level, at least in the Redwing and cowbird, in apparently the same way. It would be of considerable interest to know whether a comparable display is given by other icterids which have a striking color pattern in the cloacal region, such as the Black-billed Oropendola (*Xanthornus augustifrons*), Green Cacique (*X. viridis*), Curve-billed Cacique (*Cacicus uropygialis*), Mexican Cacique (*Cassiculus melanicterus*), and others. Of course, the Green Cacique has an inverted display (Armstrong, 1947:144) in which these colored parts may also function.

A display in which the tail is raised and spread (or fanned) occurs in the Baltimore Oriole, but in this case the display is given (so far as has been observed) while facing the stimulus object, and the striking dorsal pattern of the rectrices appears to be significant.

On 9 June 1958, at 2:30 PM, I briefly observed a tail-raising display in this species when a male flew down to the ground near a dummy female oriole which had been placed on a lawn in a "normal" posture. As soon as the male came into sight he appeared to be responding to the dummy and directing his attention to it. At first he appeared alert, with quick movements, compressed plumage, and with body held low and tail parallel to the body. He hopped about in this manner giving a soft *whit* call repeatedly and a harsher *brrr* call, both of which seemed to denote alarm or anxiety. Then, facing the dummy, but still some distance away, he lowered his body almost to the ground and cocked his tail, fully spread, straight up and held it there for a few seconds. Then, reverting to the earlier pose, he gave a long outpouring of song in the manner of a Catbird (*Dumetella carolinensis*), with squeaks, rolls, *whirr*'s, and intermittent chatters. During this continual song the tail was frequently lifted momentarily.

SEXUAL BEHAVIOR

I have not been able to determine the behavior patterns that are associated with pair formation in the Yellowhead. The male's initial behavior to new

females appears similar to that directed to his mate. For the most part, as in the Redwing, the female simply appears on the male's territory and either stays or leaves. The male gives Song-spread, engages in territorial disputes, etc., and "courts" the female. Courtship behavior or Symbolic-nesting is primarily male behavior apparently directed to the female but usually oriented away from her. The female's role in Symbolic-nesting is mainly passive. The male similarly "courts" newly arrived or unestablished females as they fly overhead or when perched nearby. Sexual-chasing also occurs during this period but it is restricted to an already formed pair. Symbolic-nesting and Sexual-chasing are the two chief aspects of intersexual relations prior to nest building. Both also occur, but to a lesser extent, following nest building. The chief intersexual behavior during and following nest building is Mating or Precopulatory Behavior; this behavior is evident in both the male and the female and, of course, leads to copulation. Throughout the period of association of a pair, agonistic behavior, apart from Sexual-chasing, which appears to have some agonistic connection, is also evident; it consists primarily of hostile behavior of the male to his mate.

Courtship or Symbolic-nesting.—Descriptive terms which were applied to the courtship behavior of the male Red-winged Blackbird are "Symbolic Nest-site Selection" and "Symbolic Nest-building" (Nero, 1956:21). These terms may be appropriately applied to quite similar behavior patterns of the Yellow-headed Blackbird, which may, however, be conveniently covered by the single term Symbolic-nesting. This term has been applied to a sequence of male behavior or aspects of the sequence in which, at least in its extreme form, the male performs nest-building movements, although the female alone builds the actual nest. Other movements which occur more often are linked (in a "complete" sequence) to the nest-building movements and are suggestive of nest-site selection behavior. Various aspects of Symbolic-nesting may be recognized in the Chaffinch (Marler, 1956:74, etc.), as well as in many other species (Nice, 1943:178–179). The sequence of Symbolic-nesting in the Yellowhead includes the following displays or movements: Elevated-wings, Flapping-flight, Dropping, Crawling, Bowing, and Pecking or Building. It seems useful to use the term Symbolic-nesting even though further study may show that some aspects of the sequence are not really related to nesting behavior. For example, the Elevated-wings display may have originated or may actually function in an agonistic sense. Included below are (1) a general description of Symbolic-nesting, followed by (2) a more detailed description, and (3) a comparison with similar behavior of other icterids.

(1) Symbolic-nesting includes the most noticeable display, apart from Song-spread, of the Yellowhead, appearing at first glance as a display of the wings, often accompanied by a slow and awkward short flight. Wetmore

(1920:403) stated: "In the most common display the male started towards the female from a distance of 30 or 40 feet with a loud rattling of his wings as a preliminary. The head was bent down, the feet lowered and the tail dropped while he flew slowly toward his mate. The wings were brought down with a slow swinging motion and were not closed at all so that the white markings on the coverts were fully displayed, the whole performance being reminiscent of a similar wing display of the Mocking-bird [*Mimus polyglottos*]." Linsdale (1938:133) also noted certain aspects of the display: "Another elaborate display often accompanied the song of the male. In one form of this display the tail was spread, both wings were raised high over the back, and the body feathers were raised. The birds seemed to have difficulty in maintaining a balance during this performance."

A closer look reveals a definite pattern of even more elaborate form. Briefly, the male raises his wings over his back (Elevated-wings), flies slowly and awkwardly for some distance (Flapping-flight), then suddenly Drops down into the vegetation where, still holding his wings upright, he Bows and then awkwardly Crawls through the vegetation with tail down and spread, often stopping to Bow and Peck (Fig. 3). This sequence of behavior is usually given in the presence of the mate or to new females, either perched within the territory or flying by. Most often the male flies away from the female and Bows while facing the opposite direction from her, but the male may also Drop near the female, or even approach her. Usually the female follows the male as he Crawls, and she faces him from nearby as he Elevates his wings and Bows. At times this display may immediately precede precopulatory behavior but it is then given rather abruptly. In one case a female was seen to go into slight precopulatory behavior—tail and head up—after following the male. Usually, however, Symbolic-nesting is not directly connected with precopulatory behavior. Song-spread display may occur during or before the Elevated-wings display and at these times the wings are not lowered as usual but are kept erect. Symbolic-nesting is most common during the period preceding nest construction. It may also be given in noncourtship situations, such as when the female is alarmed by a disturbance at the nest. Often, only portions of the sequence, especially Elevated-wings and the Flapping-flight are given. Some illustrative field notes follow:

12 May 1957, 6:20 AM: Male with female—flies away from her with slow, flapping flight and noisy wings, then suddenly Drops onto the cattails to pose with wings held upright—in this pose he Bows and then Crawls rapidly through the cattails; the female follows him, her tail and head held up momentarily in precopulation.

24 May 1957, 6:30 AM: Female in nest-lining stage. She returns to the territory with a billful of fine stems, giving a *grrk* call note to which the male responds at once with Song-spread; he then flies toward her in slow flapping flight, Drops into the cattails

near the nest with elevated wings, disappears in the cattails, then comes out and moves away.

29 May 1957, 5:50 AM: A male elevates his wings and tips forward (Bows) when a a female flies overhead.

19 May 1958, 7:30 AM: A male flies rapidly toward his female, she leaves the territory, he gives Song-spread. She returns, he flaps past her with slow flight, lands on top of the cattails with wings elevated, bows stiffly (with "Growl"?); as she moves closer he Drops into the cattails still holding his wings upright.

20 May 1958, 7:41 AM: Male raises wings high over back, flaps to a new position, Crawls through the cattails with wings upright; he burrows down out of sight—the female comes over and follows him.

(2) The Elevated-wings display is usually symmetrical, both wings being held and moved in about the same way; since the entire wing is moved as a unit an awkward flapping appearance results. Flapping usually begins while the bird is perched, suggesting flight onset. One can readily predict when a bird is about to fly by the extent of flapping, although often the wings may be elevated and flapped sporadically (and without the rest of the sequence), presumably as the level of intensity rises and falls. On one occasion observations were made of an individual which showed gradually increasing intensity; at first the primaries quivered slightly, then the wings were lowered and gradually held out from the body, and slowly, with slight shaking, raised higher and higher until they were above the level of the body. Increasing intensity of the display is apparently indicated by the higher position of the wings. Ordinarily, the wings are first brought up above the body and held in that position before the bird flies, but occasionally this display may arise during normal flight. At this time the beat of the wings is suddenly considerably slowed. The slow, awkward, or impeded flight during the display sequence (at which time the white patches are quite noticeable), has been termed Flapping-flight; it is noticeably different from normal slow flight.

It should be noted that the tail is fully spread throughout Flapping-flight (in the Redwing, too) and this may also affect the flight. The peculiar V-shape of the tail of the Common Grackle in courtship display and at other times (see Bent, 1958:397) may be related; Eyer (1954:51) thought it was an adjustment for slow flight. (However, Ficken, 1963:69, suggests that the V-tail is "probably a long-range sex-recognition character.") The Red-collared Whydah (*Euplectes ardens*) of Africa also has a slow flight display associated with courtship in which the long tail is deeply keeled, evidently in the same way as in the grackle (Emlen, 1957:209).

Occasionally, a distinct but muffled, rattling sound, possibly produced by the primary quills, may be heard during Flapping-flight. Wetmore (1920:403) and others have mentioned this; Linsdale (1938:132) said that "the dull whistle made by the wings could be heard distinctly for 50 yards or farther. . . ." The ordinary heavy wing flapping during this flight display is noisy, but the apparent quill rattling is quite distinct. Skutch (1954:263) notes something similar for the Yellow-tailed Oriole (*Icterus mesomelas*): "Often while flying it makes a crashing sound, apparently with its wings." He also re-

ports a noisy flight for the Giant Cowbird: "The flight of the males of many species of the troupial family is accompanied by a characteristic sound made by the passage of the wind through the primaries. This does not depend entirely on the size and weight of the bird, for the wings of some of the smaller orioles are resonant in flight. The sound made by the male Giant Cowbird as he flies is particularly loud, and of a peculiar quality suggesting that his feathers are stiff and vibrant" (op. cit.:316). It has been described for the Wagler Oropendola by Chapman (1928:133), who states that it is "evidently produced by the passage of the widely radiating, emarginate primaries through the air." So far as I could determine, there was no specific situation in which the sound was heard, although a few times it was noticed that the flight was directed toward a new female. Once it was given at the onset of a sex chase (see below) and there was some suggestion that it was directed to neighboring males. I think that it may be given in moments of high intensity, functioning to attract attention, and emphasizing the flight.

The Flapping-flight usually carries the male to a spot where he then Drops and Crawls, but often, depending on the situation, two or more rapid flights from point to point with wings constantly elevated may occur before a male stops and Crawls. As soon as the male Drops down onto or into the vegetation (e.g., bulrush or cattails), and this is usually done precipitously, he Bows, slanting his body and head downward. Since he often lands with wings Elevated (frequently most extreme at this point) he sometimes appears to be losing his balance and toppling forward. The spread and lowered tail probably acts somewhat as a brace or balance. At times he lands with wings outspread or even down. Bowing may be hurried and awkward or slow and precise and sometimes may be rapidly given more than once (up to three times). Occasionally Bowing occurs without any preliminary flight. In fact, the whole sequence of Elevating, Flapping, and Bowing may be given while perched. This happened several times when a male hurriedly displayed to a female flying rapidly overhead.

Immediately following Bowing the male begins Crawling through the vegetation, often working through dense clumps. Throughout this behavior the wings are held upright. After Crawling a few feet the male often stops, Bows again, and Crawls to a farther point. Usually he then stops displaying (remains quiet sometimes) and quietly emerges to rest on top of the vegetation at that spot or else returns to a favored perch. Although difficult to observe because of the situation, sometimes the male indulges in a further display associated with this pattern, called Symbolic nest-building in the Redwing (Nero, 1956:23–26). During Bowing the male may pick at bits of the vegetation or perform other movements suggestive of nest building; this suggests that Bowing behavior may be related to the motions of nest building. This is the usual behavior and it is probably the basis for the following reports. Wheelock (1904:510) states: "In a few rare instances I have known

him to make a pretence of nest-building a few feet away from the real cradle, either to amuse himself or to deceive me, for the loosely woven affair was never regarded seriously by the female. She sometimes perched near it, regarding with amusement the masculine attempt at housekeeping, and with a scornful flirt of her tail went back to her own cosy nest." Ammann adds (1938:116) that he observed males casually pecking at a few strands attached loosely to the reeds near finished nests.

Sometimes, as in the Redwing (Nero, 1956:23), an actual nest may be used in connection with the display:

22 May 1957, 5:45 PM: One male, which is still without a female, returns to his territory and lands on an old nest, sits quietly giving Song-spread; picks at the outer shell of the nest and inspects the interior (just as on the previous day). The nest is well below the level of the cattails.

6:08 PM: He returns to the territory and again lands on the old nest; sits on the edge of the nest, singing, for several minutes.

6:40 PM: He returns to the territory with Flapping-flight, lands hard on the edge of the nest, Bows into it with wings outspread, then sits above the nest and gives Song-spread, full but with no wing movement.

6:50 PM: He returns again to the territory (having gone off somewhere as before) with a flourish—obviously excited—along with several females which have come back from feeding; the females all go elsewhere and as they fly by him, he repeatedly Bows; later, as another female flies overhead, he Bows and Crawls excitedly toward the nest.

24 May, 6:05 AM: He is on the nest! Gives Song-spread, hops on the edge of the nest, lifts tail? Hops off and down into the cattails.

The behavioral sequence of Symbolic-nesting of the Yellowhead (Elevating, Flapping, Dropping, Bowing, Crawling, and Pecking or Building) is remarkably similar to that of the Redwing. I have been able to detect only two distinct differences. "Quill-rattling," as in the Yellowhead, has not been observed in Redwings, and, on the other hand, the "growl" vocalization of the latter species, given during the Bowing phase, seems not to have a parallel in the Yellowhead. On some occasions I was almost sure I had heard a slight, harsh note given at this time by displaying Yellowheads, but more often there was no sound apparent even though I was close to performing birds. If it is given by Yellowheads it must be very soft and very slight.

(3) Elements of the sequence of behavior termed Symbolic-nesting appear to occur with varying emphasis (and related plumage patterns?) in several icterids and this suggests that it may be a basic pattern of behavior in this family. Friedmann (1929: 344) was aware of certain similarities, stating: "This type of display, i.e., ruffling the feathers and bowing or bending forward, is common to many Icteridae such as *Agelaius*, *Quiscalus*, *Xanthocephalus*, *Cassidix*, *Cassicus*, *Ostinops*, *Gymnostinops*, etc., so that there is a definite tendency in the whole family to develop this type of courting attitude." And Skutch (1954:334) pointed out that in this family "there are certain widespread

types of display which appear with modification in diverse genera." Because of a paucity of information and because of the difficulty of interpreting published material, much of it predating the period of behavioral studies, it is difficult to make a comparative study. Part of the confusion in the literature results, of course, from a tendency to lump all behavior between male and female under "courtship," and in many cases in the field one can do little else, especially when viewing birds for which the stage of the breeding cycle may be unknown. Courtship and Mating appear to be two distinct features in the Yellowhead and Redwing; one would expect a similar situation in other icterids and I have attempted to assess the literature on this basis.

First of all, one can state that there is a striking similarity between the courtship display of the Redwing and the Yellowhead, the essential difference being that the Yellowhead tends to spend more time on top of the cattails with elevated wings, so that a general impression is obtained of a great deal of Elevating and Flapping display. The Yellowhead also tends to Bow more often, at least while out in sight, than the Redwing; its displays, in short, are more conspicuous. The courtship display of the Tricolored Blackbird seems to be very similar to that of the Redwing and Yellowhead (Lack and Emlen, 1939:226), although it is given more commonly than in the Redwing (Gordon H. Orians, pers. corresp.).

There is no indication in the literature that the Common Grackle gives Symbolic-nesting as such; however, the extensive symbolic building which has been observed in this species (Peterson and Young, 1950:467; and especially Eyer, 1954:59–61), and other behavior, suggests the existence of the complete pattern. Eyer (loc. cit.) indicates that abortive building by both male and female is chiefly seen during a period of a week or so after selection of the nest site. After the female begins actual construction of the nest the male continues to follow her and "guards" her, accompanying the female on nearly every trip to get nest material, "following her with his courtship flight in its extreme form." The display flight of the Common Grackle seems to be a simple form of the Flapping-flight (in Symbolic-nesting) of the Redwing and the Yellowhead. It is also possible that the extended aerial displays of the meadowlarks and the Bobolink are similarly related.

Although at first glance the well-known display of the Brown-headed Cowbird may not appear to resemble Symbolic-nesting as described in the Yellowhead, I am convinced that it is directly related. In the cowbird, Song-spread regularly is immediately followed by Elevating and Bowing, so close as to be almost one, but the distinction still can be made: Song-spread is marked by the "bubbling, guttural notes . . . *bub ko lum* . . . after this . . . begins the display proper . . ." (Friedmann, 1929:164). Then, with fluffed plumage, the bird raises its wings, sometimes more than once, and topples forward or Bows. It is this part of the display which I relate to Symbolic-nesting. What is missing, of course, is chiefly the slow flight to a potential nest site, and this may be related to the parasitic habits of the species, that is, the male has no nest site to which to fly. The relationship of similar displays of other cowbirds, as, for example, the Shiny Cowbird, to that of the Brown-headed Cowbird, is fairly clear.

The inverted display of the Montezuma Oropendola and Green Cacique (for illustrations, see Skutch, 1954:288, and Armstrong, 1947:144) can also be related to the Elevating and Bowing of the Yellowhead in just the same way. (More so to the cowbirds, of course, since in the Brown-headed Cowbird the display occasionally carries the bird quite upside down.) Gilliard (1958:375) describes Montezuma Oropendolas as ". . . hanging completely inverted, at the same time waving their wings." It has occurred to me that if Yellowheads nested high in trees as do oropendolas, instead of

in marshes, then the resemblance would be even more apparent. The Yellowhead flies slowly across the marsh, displays with Elevated-wings and some Bowing, and then drops out of sight in the nesting substrate where it gives its deepest Bowing display. On the other hand, the oropendolas nest high in trees; the more noticeable aspect of a similar sequence of behavior would certainly be the latter part, and I think that this is what has been described. Judging by the number of species which have a "noisy flight," including oropendolas, the slow flight to a potential or actual nest site may be more prevalent in the Icteridae than the present reports indicate.

Of course, as previously pointed out (Friedmann, 1929; Nero, 1956:24–26), some male icterids (Bay-winged Cowbird, *Molothrus badius*, and Shiny Cowbird) occasionally do build nests. On this basis one can expect to find a range of behavior among these birds from normal nest-building behavior by the male to ritualized patterns which have evolved from nest-building movements. Hence the term Symbolic-nesting may not apply equally well to all. It is also likely that certain elements of this sequence will have been selected out and emphasized, and others dropped, thus deleting, so to speak, portions of the pattern. Nevertheless, with this in mind, it should be possible to build a comparative scheme around this framework.

It is also clear that elements of Symbolic-nesting may function in slightly different ways in different species. The display of the Brown-headed Cowbird, judging by Laskey's observations (1950:161), appears to be directed toward other males as an intimidation gesture. This may partly explain the occurrence of displays by various male cowbirds in the absence of a female as noted by Friedmann (1929:325).

Beecher (1953:326) calls attention to the adaptive convergence of African weavers and American blackbirds, some of which have a very similar plumage (e.g., *Agelaius phoeniceus* and *Euplectes axillaris*) and nest in colonies in similar habitats. Emlen's description (1957) of the courtship behavior of several species of *Euplectes* suggests that there is a close similarity in courtship habits as well. He describes two types of courtship behavior directed toward females: a simple pouncing flight, and a perch display. Essentially, a slow flight characterized by plumage display ends by a sudden terminal drop or pounce into the grass, where a perch display is then assumed. I think that this can be equated with Symbolic-nesting as described above for the Icteridae. Skead's recent description (1959) of courtship behavior of the Red-shouldered Widowbird (*Coliuspasser axillaris*) (equals Red-shouldered Whydah, *Euplectes axillaris*) shows an even greater similarity: after a flight across the territory with feet suspended and wings in a "'rowing' revolving action" at times, the male suddenly dives into the grass with wings extended, near a female or some distance from her, "as though inviting her to the place." Once down in the grass he evidently weaves the outline of nest frames and presumably the female is invited to make use of these. The similarity of plumage between this species and the Redwing, as pointed out above, is often mentioned as an outstanding example of convergent evolution; it is therefore of interest to note the similarity of behavior in these two birds.

Sexual-chasing.—Pursuit of the female by the mate alone or by the mate and an accompanying group of males is common in the Yellowhead and appears similar in all respects to that which has been described for the Redwing (Nero, 1956:26). A pair is nearly always the basis for a chase, which appears to be chiefly agonistic behavior arising out of the courtship situation. (Ammann, 1938:102–103, states that males attempted to copulate at the close of

sex chases but this was not supported by my observations.) Chasing was observed practically throughout the period of observation. Frequently, chases arose through activities of the female which brought her into prominence, for example, flights carrying nest material, quarrels with other females, sudden return of the female to the territory, etc., but often chases seemed to be suddenly initiated by the male. Chases ended abruptly as the male withdrew or captured the female. In six cases (out of 26 recorded chases) the male caught the female and held onto her rump feathers (once in midair); each time both birds ended up in the water. Most chases were limited to the territory but occasionally went outside it. Group chases, involving two or more males, occurred nearly as often as single chases. Paired birds were involved in most episodes, but a few times strange intruding males or wandering females initiated chasing. Aggressive behavior seemed to predominate in the male during chasing and occasionally a vocalization was given which also seemed aggressive—once the "hawk call" and rapid song, and once a call resembling female alarm. Twice females were recorded calling—once a harsh call (similar to the aggressive screech given to other females) and once definite scolding notes. Aggressive behavior by the male to his female is frequently seen and does not always lead to chasing but is probably a part of the pattern. Males rather constantly strike at their mates or show signs of aggression when the females quarrel or even merely sing to other females, especially new ones (on the territory) which the male may be courting. Again, this is quite similar to that which has been reported for the Redwing. (In 1958, a female Redwing was frequently attacked, when she sang or scolded, by a Yellowhead male from an adjacent territory.) The following field notes illustrate Sexual-chasing and some of this aggressive behavior:

12 May 1957, 6:45 AM: A male suddenly chases his female, she gives a nasal *hah-hah* like the aggressive screech to other females, and they fly rapidly around the territory three times, and then stop suddenly.

24 May 1957, 7:15 AM: Female B returns to the territory from a long distance flying about 5 feet above the cattails and carrying a long piece of grass; Male B at once withdraws from an encounter with another male out on the edge of the territory to drive at her—he chases her out of the cattails and into the air with noisy wings, he then suddenly leaves her.

8 May 1958, AM: Female attacks a dummy female, her mate chases her into an adjacent territory, and then the owner of that territory comes flying over with flapping wings (displaying to the female?), which leads to a group chase involving four males; it finally breaks up on the first territory.

9 May 1958, 6:50 AM: A male Bows and Elevates to newly landed female, and then strikes at his first female, which repeatedly drives at the new female. The male is quick to strike at his mate when she moves toward the new bird. He Bows deeply; the new female stays hidden in the cattails.

9 May 1958, 6:55 AM: A male seizes his female after a short chase, they end up partly

in the water—he holds her by her back feathers while she flounders and gives alarm screech—he suddenly lets her go.

19 May 1958, AM: A male drives at his mate with a harsh call when she lands (too) close to a new female.

Precopulation and copulation.—I observed copulation six times on the following dates in 1957: 24 May (7:45 AM), 29 May (6:05 and 6:15 AM); and in 1958: 9 May (7:07 AM), 19 May (5:00–5:30 PM—two). Attempted copulation or precopulatory behavior was recorded on 28 other occasions. Precopulatory behavior and attempted copulation in response to a dummy female was observed and filmed on 3 June 1958; the behavior in this situation appeared to be similar in nearly all respects to that which was earlier observed under normal conditions.

Precopulatory behavior of the female Yellowhead is generally indicated by a posture similar to that of the Redwing and other icterids: the tail is raised, the bird crouches on its tarsi with breast lowered to the ground, the head withdrawn with bill pointing upward, the wings held out and shivered (a combination of movement of the primaries being rapidly spread and closed while the whole wing is raised or lowered), and there is a vocalization (with open bill). At high intensity the tail is held nearly vertical, the rump is higher than the head, the precopulation call is constant, and wing shivering is rapid. Various degrees of display indicate increasing and variable intensity; no vocalization, short sporadic displays, display without movement, momentary wing shivering, etc. As in the Red-winged Blackbird, in initial precopulatory behavior, or very early stages, occasional slow, hovering flights occur (with rapidly beating wings held mainly below body level), sometimes while carrying nest material. On one occasion when a female was in precopulatory slow flight a low, continuous "whirring" sound was heard which was evidently produced by the wings. Once (19 May 1958) a female flew a short distance while giving the precopulatory display (tail and head up). The female had been in precopulatory behavior on the cattails; her mate approached aggressively and she then flew off away from him in the same pose —a very unusual appearance. This has also been recorded in the Redwing (Nero, 1956:32). Tail-raising and Wing-quivering are sometimes given alone.

There is a peculiar relationship between female precopulation and an apparent appeasement display (see Tail-lifting). Frequently, the female lifts her tail as the male approaches her in aggressive display or movement, and her behavior seems to deter him. In one instance a female was seen to raise and then lower her tail (no other display) as her mate suddenly flew past and behind her. Except for the appearance of this same behavior between aggressive females it might have been overlooked and considered to be low-intensity precopulatory display brought about by the aggressive approach of

the male. On the other hand, what appears to be low-intensity female precopulation often draws an aggressive response from the mate, and occasionally a subsequent aggressive reply from the female. For example:

19 May 1958, 4:15 PM: Female in precopulation, her mate drives at her aggressively and forces her into the water, both come up wet. A moment later she returns to the territory; as soon as she lands she gives signs of precopulatory display; approached by her mate, she is in precopulation; he comes in aggressively and she turns to bite at him. She goes to build on the nest—he sits off to one side.

Similarly, a female in precopulation may suddenly stop giving this display at the approach of the male. An even more complete response by the male may be met with aggression from the female:

20 May 1958, 8:21 AM: Female returns to her territory giving an excited call, her mate at once goes into slight Elevated-wings and Crawl, then, by a rapid, hopping movement approaches the female who is sitting up high on the cattails in precopulatory display; the male moves about her then he reaches toward her (with neck extended) at which she pecks at him, and so it ends.

27 May 1958, 6:45 AM: Female with tail up, head back, wings out (precopulation) but sitting still: male approaches her, droops his wings somewhat, gives a song, Hops about female, moves toward her posterior and she faces about to peck at him, he jumps back and it ends.

7:30 AM: Female in precopulation, male flies to her, and she drops the pose, then, as he approaches aggressively, she raises her tail and runs off; as he nears her she pecks at him, and he leaves.

8:01 AM: Female in precopulation, male approaches and female turns to peck at him.

I presume that this situation is one of lack of synchronization or lack of readiness to copulate by one or both. In the Chaffinch: "As the season proceeds the female, although constantly aggressive towards female rivals, becomes more so towards the male, with a sudden increase in intensity at the start of nest building. . . . This continues right up to the onset of copulation, though once the female solicits fully, attacks on the male usually become uncommon . . ." (Marler, 1956:116). Unreceptive female meadowlarks "assumed a semi-crouch position, with feathers held tight against the body and bill gaped and pointed directly at the advancing male. From the latter posture, the female could further repulse her mate with pecking gestures" (Lanyon, 1957:39).

Female precopulation (low and high intensity) also brings about other responses from the male (aside from full male precopulation, below) which presumably indicate a low response in the male, namely, Symbolic-nesting or parts of it (Elevating, Bowing, Flapping, Dropping, Crawling). Occasionally males responded with Flapping-flight and "quill-rattling," and extreme Song-spread. Sometimes female precopulation was even apparently ignored by the mate.

Male precopulatory behavior usually originates in response to precopulation of the female. Since usually the male is some distance from the female when she begins to display he must first approach her. In doing this the male typically flaps heavily to the ground (or lower level of the marsh vegetation) or across the cattails closer to the female. Then, with wings only partly out or raised, with head hunched and bill down, tail spread and down, back feathers erected or often lifted (very similar to Crouch-bristling), he runs rapidly (if in the open) or climbs awkwardly over objects in his path to approach the female. Occasionally male behavior appears to be elicited by remote stimuli as indicated by the following note:

> 29 May 1957, 6:30 AM: Male flies slowly from his territory to an open field nearby. He lands and then at once raises one wing high and with head down runs rapidly along on the ground in the direction away from the territory for about 60 feet—a startling performance since no females are apparent. A few minutes later a male (same?) flies slowly toward some females feeding on the ground far away from the slough—when about 50 feet from them, he raises both wings high overhead and Drops straight down, landing like a butterfly with both wings still held stiffly upright—then, with head down, he moves along the ground with one wing upright and the other out sideways as if for balance. This looked like incomplete precopulatory behavior.

Wetmore (1920:403) stated: "Or they clambered stiffly along, hobbling over masses of bent-over rushes, with heads bent down, tails drooping and back humped, appearing like veritable clowns." When approaching a female perched upon the cattails, there is, of course, more use of the wings, though they are never spread out in display as in the Redwing. Song-spread may be given occasionally during the approach. This is considered the "first phase" of precopulatory behavior (Fig. 4). In the Redwing this leads directly to mounting (Nero, 1956:32–33). The Yellowhead sometimes mounts directly following this behavior, but usually some part of the following behavior, here called "second phase" precopulatory behavior, occurs (Fig. 4). The male, when within several feet of the female, may rapidly hop up and down on flexed tarsi, alternately springing away and back again, and around or toward her in a hunched or upright posture, pause briefly at her side to scratch at her back with one foot, move around to her posterior, then, with flapping wings raised high, quickly mount. Finally, in copulation, the wings are flapped vigorously, the tail is thrust down and the neck is stretched up but with the bill pointed down (Fig. 5). Copulation usually occurs several times in succession, the male dismounting, hopping away (sometimes in front of her) and circling back and remounting, up to a dozen times or more and usually not less than three or four times. In one case a male mounted a female eight times or more in less than half a minute. Specific notes on precopulation and copulation sequences follow:

20 May 1958, 7:47 AM: A male flaps heavily to ground near a female, approaches her with a very rapid run, hunched, wings not spread—near the female (which is in precopulation pose) the male frenziedly jumps up and down and around in a circle (not around her). Once he spread out his wings (Song-spread?) while standing near the female. He leaves. Female had been in precopulatory pose throughout.

24 May 1957, 7:50 AM: Suddenly see male and female in action in field near marsh—female in full precopulation—male approaches her bristling, with bill down and sidling (looks just like behavior given earlier this morning to an intruder male). He reaches out one foot and claws at the back of the female, mounts partly, then off, back around to the rear of the female as she goes from an aggressive posture with open bill to full precopulatory display. It ends incomplete.

27 May 1958, 7:20 PM: Female in precopulatory pose but standing up high—male comes toward her, crouching and with wings partly out and dragging, when close he holds his head higher with the yellow feathers all erect and hops about in front of the female, then at her side—it just ends when the female suddenly drops her pose.

29 May 1957, 6:05 AM: Female on ground in precopulation, male feeding about 20 feet away—no apparent sound from the female but the male suddenly walked over, bristling, by her—as he neared her he clawed at her back with one foot, then mounted and copulated, thrusting his tail down against her body—he jumped off on the left side, circled to his left and back to remount again, all very rapidly, and remounted at least eight times.

Observations of an incomplete sequence recorded on film suggest that clawing of the back of the female by the male is related to conflict of escape and copulation tendencies. The male's quick retreat at her first movement is indicative of his escape tendency which is presumably related to her aggressive behavior at this stage, as has already been noted. No doubt, the escape tendency is stronger in the male until the full precopulatory posture and behavior is assumed by the female. In the Brewer's Blackbird "copulation does not ensue unless at the male's close approach she stops the wing action and stands rigid" (Williams, 1952:6).

Movies made of precopulatory response by a male to a female dummy afforded additional details of this behavior which appeared to be similar to behavior under normal conditions. In one sequence, in the curious Hopping, the male crouches deep on his tarsi with breast feathers touching the ground, back feathers erected, and bill down. From this position he suddenly springs upward, turns sideways in the air and lands several inches away on his tarsi again, drops his throat to the ground, then springs sideways, thrusting up from the "prone" position to come down in the same manner; when he lands two hops from the dummy, he has his head up and proceeds to hop in the upright posture toward the dummy, the yellow plumage of the head and throat strongly erected (Fig. 4, upper middle). With one more upright hop he is at the side of the dummy, standing at full height and reaching out one foot to scratch at the back of the dummy (Fig. 4). Occasionally he walks about between "bounces." At a distance he hops in the crouched or prone position but as he gets closer he gradually gets more upright, finally standing fully upright at the side of the dummy.

The peculiar hopping by which the Yellowhead male sometimes approaches the female in precopulatory display has no obvious parallel in the Red-winged Blackbird, but something similar has been noted in several other icterids. Hudson writes (*in* Friedmann, 1929:40) for the Screaming Cowbird: "'. . . with tail and wings spread and depressed, the whole plumage raised like that of a strutting turkey-cock, whilst the bird hops

briskly up and down on its perch as if dancing.'" Friedmann (op. cit.:41) notes that this species "hops up and down on its perch . . . the male kept getting closer to the female with each jump. . . ." An even likelier description is given for the Shiny Cowbird although it was considered an unusual variation: "A male was chasing a female and the latter flew on to a fence post. The male then lit on the fence wire about three feet from the post, fluffed out all his body and head feathers, bent his tail forward and under, and arched his wings to nearly a horizontal position. Then he bent forward very slightly and suddenly jumped up into the air and lit on the same wire about ten inches nearer the female than before. No sooner had he touched the wire than he bounced up again, coming down just about a foot nearer the female. Again he bounced up and landed very close to her when she flew off and he followed. During the entire performance he maintained the same position that he assumed before the first bounce" (Friedmann, op. cit.:70).

Similarly, Chapman (*in* Friedmann, op. cit.:323) observed for the Red-eyed Cowbird "'. . . occasionally one would rush up to another with a series of bouncing hops. . . .'" And Friedmann (1925:549), describing behavior of a male of this species to a female stated: ". . . bent his head so that his bill was touching the feathers of his breast for its full extent. Then he suddenly bounced up and down four times, each bounce taking him about an inch from the ground. . . . In its habit of bouncing up and down it resembles two Argentine species (*Molothrus bonariensis* and *Molothrus brevirostris*) more than it does *M. ater*." Skutch (*in* Bent, 1958:459) also notes this behavior in the Red-eyed Cowbird. Skutch (1954:318) uses nearly the same words to describe the behavior of a Giant Cowbird.

It is difficult to tell if there is any similarity, but Bendire (*in* Bent, 1958:221) says of the Hooded Oriole (*Icterus cucullatus*): "'. . . a male in second-year plumage was observed hopping round and round his mate in a tree. . . .'" An observation by Tyler (1923) of behavior of a Baltimore Oriole may also be related.

Hopping may arise primarily when the sexually aroused male is thwarted by an unreceptive female. Skutch (op. cit.:320) has indicated that the female Giant Cowbird is usually indifferent, or hostile, to this display by the male. Also, considerable variation in the extent of this display has been noted in the Red-eyed Cowbird by Friedmann (1929:324). This is also true of the Yellow-headed Blackbird; in this species Hopping occurs typically in incomplete sequences of mating, rather than when copulation actually ensues; in five observations of sequences leading to completed copulation, Hopping was seen only once; it was seen on five other occasions, however, in incomplete sequences. And it occurred repeatedly when a male was responding to a female dummy. On one occasion it occurred and at great length even though the female appeared to be completely receptive. The origin of the Hopping display may be explained as a conflict between the sexual tendency and the escape tendency. The "wary" scratching of the female by the male prior to mounting, and the quick retreats in the face of the female's aggression would seem to substantiate this belief. It is of interest to note that copulation in the Yellowhead usually involves several successive mountings, whereas in the Redwing, where this display has not been observed (even though copulation was elicited in numerous experiments with dummies), copulation is invariably attained by one or two mountings. The upright posture with arched neck, etc., when close to the female has been described for other species. Lanyon (1957:39) says of the meadowlarks: "The male began this behavior with the basic expansion posture but the crown feathers were more obviously erect. He strutted about in the vicinity of the female, holding his body more erect than during territorial encounters, with the bill pointed downward toward the

expanded chest. This 'strutting' which was confined within a radius of a few feet from the female, constituted the mating approach of the male." Skutch (1954:318), reporting on the behavior of the Giant Cowbird, states: "Approaching a female, he would plant himself squarely in front of her and draw himself up until he towered above her and seemed to be thrice her height. Arching his neck, he depressed his head until his bill rested among the out-puffed plumage of his breast, and he erected the feathers of his cape until they surrounded his head as an iridescent black ruff, in the midst of which his red eyes brightly gleamed."

Scratching of the back of the female by the male in mating behavior has been reported for at least one other icterid, the Western Meadowlark. According to Lanyon (1957:40) a male approached its mate, "pawed her back momentarily with vigorous scratching motions of his feet and then mounted." Also, Robert W. Ficken has taken movies which show this behavior in the Common Grackle.

The "first phase" of Yellowhead precopulatory behavior (i.e., running toward the female in Crouch-bristling) is apparently analogous to the "'crouching lopsided' posture" of the Chaffinch, and "second phase" (Hopping back and forth in crouched posture, then upright posture, etc.), analogous to the "'upright lopsided' posture" (Marler, 1956:104–107). According to Marler, in the former display both escape and aggressive tendencies appear to be active while a copulatory tendency is not yet in evidence; the latter display shows an increase in copulatory and escape components. Note the similarity between the hopping "dance" of the Yellowhead (in "second phase") and the "'precopulatory dance'" of the Chaffinch (op. cit.:120). Several members of the genus *Coliuspasser* bob or pump the whole body up and down in precopulation apparently in a similar manner (Emlen, 1957).

Summary of precopulatory and copulatory behavior and comparison with other icterids.—Precopulatory behavior of the Yellowhead in its "first phase" consists of a hunched and crouched posture with wings held out to some extent, tail broadly spread and down, and fluffed or erect plumage. Parts of the plumage may be more erect than the rest. On the whole, the "first phase" of mating behavior appears to be strongly related to agonistic displays (Song-spread, and Crouch-bristling, e.g.) combining the spread tail and open wings and crouch of these with a slow and "wary" approach to the female. Attack and escape tendencies appear to be in conflict. "First phase" precopulation display of the Redwing male is very similar to Redwing Song-spread display; "first phase" precopulatory display of the Yellowhead closely resembles Crouch-bristling. In the Brewer's Blackbird Song-spread (called "Ruff-out") and the "male precoitional" displays merged imperceptibly when males responded to dummies and the two could not be distinguished (Howell and Bartholomew, 1952:140–141). Components of "first phase" precopulatory behavior may also be recognized in the Bobolink, Tricolored Blackbird, Common Grackle, Boat-tailed and Great-tailed Grackles, and several cowbirds (see Bent, 1958; Friedmann, 1929; Selander and Giller, 1961:60). Frequently this "first phase" leads directly to copulation; this is the invariable pattern in the Redwing. In the Yellowhead, and apparently other icterids (above), however, a "second phase" is common, in which as the male nears the female

he assumes an upright posture with head erect and bill depressed while squatting on lowered tarsi. He frequently Hops ("jumps," "bounces") closer to the female, while maintaining this posture, springing up from the ground and coming down again on lowered tarsi. Even in the Yellowhead, where this display is common, it is sometimes omitted or appears only briefly. This posture is apparently related to the act of copulation which it resembles in some details except that the wings are usually closed. Escape and sexual tendencies appear to conflict in this situation. The recording of this behavior for the several cowbirds and the Yellowhead suggests a common bond between these species. The apparent absence of this behavior in the Red-winged Blackbird suggests that the Yellowhead is more closely related to the cowbirds than to the Redwing, though according to Beecher (1951), *Agelaius* has stemmed from *Molothrus*, and *Xanthocephalus* from *Agelaius*. The concealed red-pigmented head and breast of *Agelaius phoeniceus*, and evidently *A. tricolor* (Nero, 1954:151–152), may indicate in addition that these species are not as closely related to the ancestral cowbird as has been supposed (Beecher, 1950:57).

Female Wing-flipping.—Female Wing-flipping as reported for the Redwing (Nero, 1956:13–16) is associated with postnesting behavior, but it is included here because of its intersexual nature. Although Wing-flipping has not been observed in the Yellowhead, one observation suggests its possible occurrence. On 3 June 1958, a female which had young in the nest and which was disturbed at my presence, became more and more "loose-winged," i.e., held her wings out from the body slightly and hanging loosely, as she became more anxious and as she moved closer to her mate.

SUMMARY

Yellow-headed Blackbirds were studied in May and June (1957, 1958) at the height of the breeding season on small marshes near Regina, Saskatchewan. Emphasis was placed on agonistic, courtship, and mating displays, and related behavior. Motion and still pictures were taken in conjunction with dummy birds used to elicit a variety of displays, though in nearly all cases these observations were supported by records of behavior in normal circumstances.

Agonistic displays of several types were recorded. Song-spread—the typical combination of plumage display and song—was given by both sexes, being directed mainly to members of the same sex. Flight Bill-tilting replaced typical icterine Bill-tilting as a common threat display given especially by males in territorial disputes. It was also found to occur commonly in the Brown-headed Cowbird, evidently occurs in the Eastern Meadowlark, but is rare in the Red-winged Blackbird. Nodding, a sudden lowering of the head with bill downward, was a male display commonly seen during aggressive encounters. It appeared to be related to submissive or appeasement display of the nape as seen in other birds. Crouch-bristling describes an aggressive "head-forward" type of display seen in both sexes; displays given by males in courtship situations appeared identical. This display is apparently similar to a courtship display of the male Redwing.

Tail-lifting appeared primarily as an appeasement display of the male in agonistic and conflict situations; it showed some resemblance to female soliciting behavior. Similar display was given by females to females, and on some occasions to males.

Courtship behavior consisted mainly of a sequence of behavior, or aspects of this, called Symbolic-nesting in which the male displayed his wings, flew away from the mate or a new female in slow, awkward flight, suddenly dropped down into the nesting substrate, and then crawled along, still with elevated wings, and then went through motions suggestive of nest building. The female tended to follow the male closely. This was similar to that which has been reported for the Redwing; portions of the sequence have been reported for a number of other icterids and it is suggested that this is a basic pattern in this family. Sexual chasing occurred during the courtship period and was also similar to that which has been reported for the Redwing.

Mating behavior of the female appeared much like that described for the Redwing. Male response consisted of a posture similar to aggressive Crouch-bristling. Copulation ordinarily included several rapidly successive mountings. The peculiar Hopping behavior, etc., has been found in a number of icterids, especially *Molothrus*, *Tangavius*, and *Scaphidura*, though not in the Red-winged Blackbird. This suggests that the Yellowhead is possibly more closely related to the cowbrids than to the Redwing, or, at least, that this behavior is primitive.

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